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MORPHOLOGY AND HOST RELATIONS OF PUCCINIASTRUM AMERICANUM

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MORPHOLOGY AND HOST RELATIONS OF PUCCINIASTRUM AMERICANUM[1]

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The orange rusts have always been considered as practically the only rusts of economic importance on species of Rubus in America. *Kuehneola uredinis*, it is true, is known to cause considerable damage to fruiting canes of certain cultivated varieties of blackberries. *Pucciniastrum americanum* (Farl.) Arth. is not rare on wild raspberries but its effects on the host have been found heretofore to be altogether negligible. Brief notes dealing mostly with its relationships to the European form *P. arcticum* have appeared from time to time but no reference has been made to damage to cultivated raspberries. An outbreak of this rust, therefore, of such severity as to cause defoliation and spotting of canes of certain varieties, becomes a subject of interest.

One of the native hosts of this rust is the wild *Rubus strigosus*, and like the orange-rusts and the stemrust, Kuehneola, the Pucciniastrum will no doubt be found wherever the natural hosts may grow. The rust has been reported rarely on *R. occidentalis*, but "*R. neglectus*," a hybrid between the red and the black raspberries, seems to be rather susceptible according to Farlow (*9, p. 13*).[2] At Bell, Md., where an outbreak occurred in 1922, Mr. G. M. Darrow has gathered together from all parts of the world a number of species and horticultural varieties of Rubus and has originated many new forms in connection with his breeding work. During July it was found that the leaves of several different hybrids were dropping off prematurely, leaving the canes entirely bare below. The lower surface of the leaves was evenly covered with uredospores, giving them nearly the same appearance as blackberry leaves heavily infected with the Kuehneola. The leaves at the growing tips were sometimes only slightly affected and the attacks seemed to increase in severity from the tips downward, showing that the rust had been present for some time.

Conical peridia (Pl. 1, C), each surmounted by a corona, were easily found on leaves just being attacked, and as the spores were identical with those found on the fallen leaves there can be no question that this defoliation was being caused by what has heretofore been considered a harmless rust. From July 28 to August 4 a survey was made to ascertain which species, varieties, and hybrids were being attacked. Mr. Darrow cooperated with the author in going over these records.

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[1] Accepted for publication Jan. 22, 1923.

[2] Reference is made by number (italic) to "Literature cited," pp. 893–894.

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Certain varieties were represented by as many as 75 plants, others by only 1 or 2, and conditions for infection were perhaps more favorable on one side of the field than on the other, so that a full report on these observations would not fully represent the actual degrees of susceptibility. Among others, the following seedlings were found to be quite badly infected: Ranere × Cuthbert,[3] Cuthbert × *R. lasiostylus*, La France × Ranere, Van Fleet × Ranere, Laxtonberry × Ranere, Cuthbert, Gregg × Cuthbert, Brighton × La France, Brighton × *R. lasiostylus*, *R. coreanus* × Brighton, Shaffer seedlings, Shiebley × King, *R. leucodermis* × King, Newman 23 × *R. coreanus*, seedlings of Hailsham open pollinated, Syracuse open pollinated, Brighton selfed. The Ranere (St. Regis) was infected, but not as heavily as were the Cuthberts.

Certain hybrid seedlings were so severely infected as to result in almost complete defoliation, petioles and canes also being attacked. These very susceptible kinds include such hybrids as June × Cuthbert, Latham × Brighton, Latham × Ranere, Erskine × Ranere, *R. coreanus* × Brighton, etc.

A number of varieties in this plot were only slightly infected, but, as previously noted, the number of plants in many cases was too small to prove that they were resistant. About 50 plants each of the following forms were carefully examined at this time, but no rust was found: *Rubus Idaeus*, open pollinated seedlings of the Mahdi (which is a cross between *R. Idaeus* and a European blackberry), *R. innominatus* × Antwerp, *R. innominatus* × King, *R. innominatus* (open pollinated seedlings). A few self-pollinated Cuthbert seedlings in this field showed no rust, but many plants of this variety in a garden near by were heavily infected.

Separated from these plots by about 40 rods was a third plot, in which several plants of wild *Rubus occidentalis*, *R. strigosus*, *R. leucodermis*, King, Cuthbert, Ranere, etc., were growing. A few pustules were found on one unnamed variety. A month later the rust was very abundant on the King, June, Newman 23, Cuthbert, and some was found on *R. strigosus*, but *R. occidentalis*, *R. Idaeus* (Hailsham variety), and 5 Asiatic raspberries were not affected.

Mention has been made of finding the rust on leaf stalks and canes. The cankers on the latter are sometimes 2 or 3 inches long. A species of Gloeosporium (not anthracnose) was also common in large cankers on the varieties whose canes were most heavily attacked by the rust. It is possible that this fungus became established in the lesions first formed by the rust; at any rate the combined effect of the two fungi will be to kill the canes. The calyx and carpels of late-fruiting or everbearing varieties were sometimes badly rusted. It is certainly curious to see the golden-yellow pustules deeply embedded in the juicy red carpels. There was more rust on the fruit of a late-flowering form of *R. strigosus* than on the leaves.

A press of work prevented a satisfactory examination of species of wild and cultivated raspberries in other localities to learn how common the rust was in the vicinity. It is clear, however, that the rust had found in these hybrids very susceptible hosts.

[3] The Black Pearl, Kansas, Cumberland, Gregg, and Plum Farmer, are American horticultural varieties of black raspberry which were originated as seedlings or by selection from *Rubus occidentalis*, of which *R. leucodermis* is a western variety; the Shaffer, Columbian, and Royal Purple are of American origin, probably derived from the form *Rubus neglectus*, which is a hybrid between *R. strigosus* and *R. occidentalis*; the Cuthbert, King, Victor, Erskine, June, Latham, Ranere, and Brighton, are American horticultural varieties of red raspberries, and related to *R. strigosus*; *R. Idaeus*, the Antwerp, La France, Laxtonberry, and the Hailsham, are European red raspberries; *R. coreanus* and *R. innomiatus* are native of China.

An inspection of the berries grown at the Government farm at Arlington, Va., was not made until the latter part of September. From 6 to 50 hills each of Cuthbert, King, Ranere, Antwerp, wild *Rubus occidentalis*, Kansas, Black Pearl, Cumberland, Plum Farmer, Shaffer, Columbian, and Royal Purple are grown. The Cuthbert red raspberry was the most severely attacked; much defoliation had resulted, and the remaining lower leaves were well covered with uredinia. Considerable rust was found on the Columbian, Royal Purple, and the Victor. The Ranere (St. Regis) and King varieties bore some rust, but not enough to cause any damage. No rust was found on any of the black raspberries grown here, and as *R. occidentalis* (at Bell, Md.) showed no rust it may be assumed that our black raspberries are very resistant. It is not strange to find that crosses between the black and the red varieties in many cases prove to be very susceptible. Whether the strain of the rust which made its appearance in the vicinity of Washington, D. C., is more virulent than that heretofore found on *Rubus "neglectus"* and *R. strigosus* is not known, but it is evident that many of the hybrids at Bell are more susceptible than either of the parents.

The host is occasionally erroneously identified by collectors, especially in the case of the red raspberry, which is often confused with the black raspberry. For example, in the Path. Coll., B. P. I., is found No. 2280, N. A. Uredinales, one gathering at Madison, Wis., October 6, 1906, and another at Mackinac, Mich., September 6, 1894, in which the host is given as *R. occidentalis* when it is a red raspberry. Arthur (*2, p. 190*) states that *R. occidentalis* was erroneously given as a host for *Pucciniastrum americanum* in Bull. Torrey Club (*1, p. 468*). In the same article a specimen from Algoma, Wis., was referred to *P. arcticum*, and the host is given as *R. occidentalis*. The rust is clearly of the *P. americanum* type, and the host is *R. strigosus*. Davis (*6*) has shown that *R. occidentalis* can be infected by *P. americanum* from *R. strigosus*. We have not found pustules of this rust on the wild black raspberry in the vicinity of Washington, D. C., but more careful search would very likely result successfully. The rust is undoubtedly more widely distributed than is commonly supposed. Specimens on cultivated raspberries have been referred to other species by mistake. In the Path. Coll., B. P. I., we find one packet of the rust on a red raspberry originally labeled *Lecythea Ruborum* Lev.; No. 32, Economic Fungi, Seymour and Earle, *Phragmidium Rubi-Idaei* (P) Wint. is *Pucciniastrum americanum*. One gathering of Pucciniastrum on *R. strigosus* was sent to the author as orange-rust in response to a request for red raspberry plants infected with the Gymnoconia.

THE MORPHOLOGY OF THE UREDINIUM

Farlow (*9*) recognized that the rust which he had found on a hybrid raspberry differed somewhat with respect to the shape of the peridium from *Pucciniastrum arcticum* of Europe. The peridium was more sharply conical than that of *P. arcticum*, which is said to be low and broad. He called attention to a good illustration of the peridium of the American form by Dietel in Hedwigia (*7, p. 331*) under the name *Phragmidium gracile*. Farlow proposed the variety name *americanum*, which Arthur (*1, p. 468*) later raised to specific rank. Davis (*5*) has shown that *Pucciniastrum arcticum* is very common in Wisconsin on *Rubus triflorus* and questioned at that time whether the differences in the morphology noted by Farlow may not after all be due to host differences. He is now convinced (*6*),

however, that the two forms are distinct and reports the work of one of his students who failed to infect *R. strigosus* with uredospores from *R. triflorus*, whereas *R. strigosus* and *R. occidentalis* were infected with spores from *R. strigosus*. The reader is not informed just what was done in the way of attempting to infect *R. triflorus* with spores from either host. The leaves of *R. arcticus* and *R. triflorus*, practically devoid of tomentum on the lower surface, are certainly quite different in texture from those of our common raspberries. No one would question that there may be, as we have shown, certain hosts that are more susceptible than others, and it is possible that differences in texture of tissues attacked by the rust could very well account for the differences or modifications in the form and size of sori which originally led Farlow to suggest that the form on *R. strigosus*, etc., be called *P. arcticum* var. *americanum*. The presence of *P. americanum* at Bell, Md., where pustules occurred so abundantly on leaf blades, midribs, petioles, canes, floral envelopes, and even on the fruit, offered a rare opportunity to study the morphology of the sorus.

Our sections show that there is a great variation in the form of the uredinia developing on the same plant. Some are sharply conical with coronate peridia; others are low and broad. Pustules were found to vary in size from 50 μ to 1 mm. in diameter. The peridia of uredinia developing on the under side of the leaf (Pl. 1, C) conform to the type described by Farlow. On the larger veins and especially on the petioles they tend to grow much larger and round out, sometimes becoming nearly globular (Pl. 1, B). The corona is not conspicuous in such peridia, especially where they are rather deep-seated, originating beneath three or four layers of cells.

Sori on canes are much flattened, elliptical or lenticular (Pl. 1, D, E, F, G, and 3, A). In such cases the heavily cutinized epidermis effectively prevents the protrusion of the peridium (Pl. 1, G), so that the peristomal cells and most of the peridium often disappear through disorganization. Spores are discharged through the passageway opened by the crushing and thrusting aside of the peridial and host cells above (Pl. 1, A).

Deep-seated sori are apt to occur in the calyx and fruit where the apex of the peridium seldom appears through the epidermis. Adjacent sori merge by the dissolution of side walls, large saclike cavities which are packed with spores resulting. Sori that do not lie much over two or three cells deep in the tissues beneath the epidermis are erect (Pl. 1, F), broadly elliptical, or lenticular. While individual sori on canes are large, they increase in length by coalescence (Pl. 1, G). Very frequently the vegetative hyphae mass together, crushing aside the host cells of the cortex. If these primordia lie near the forming cork layers, or lie deep down in the cortex, the uredinia will be inverted, the "peridium" being formed on the inner side (toward the center of the cane) (Pl. 1, D, E).

Two sori may originate from the same primordium, one having a peridium on the side toward the epidermis, the other on the side next to the cork cambium, which lies quite deeply embedded in the cortex. The sori shown in Plate 1, F, originate from separate primordia; the one above is erect, the other inverted.

ORIGIN OF THE SORUS AND ITS PERIDIUM.

The origin of the sorus is most easily studied from sections of the rust as it occurs on leaf stalks. The vegetative hyphae are not well provided with a granular or stainable cytoplasm, but the cells giving rise to the

primordium increase in size and their contents become granular and stainable and the nuclei show very distinctly (Pl. 2, A). Cells become arranged side by side in a compact plectenchyma. The terminal cells which eventually constitute the peridium elongate rapidly, lose their granular cytoplasm and nuclei by disorganization, and act as buffer cells to push aside and crush the host cells above. In Plate 2, B, two or three terminal cells at each end of the section are more heavily shaded in the drawing to indicate that they were more deeply stained than the others; the final divisions by which peridial cells arise will soon take place. In this way the sorus continues to increase in breadth for some time. In the formation of the teleutospores of species of Gymnosporangium (*8*) terminal cells of a sorus primordium function purely as buffer cells and entirely disappear as the sorus matures. It is the subterminal cells from which the teleutospore buds are formed. This is not the case in *Pucciniastrum americanum* on petioles, where the buffer peridium persists more or less and is usually recognizable in an old sorus, while the subterminal cells disappear.

Later the author will consider spore formation as found in *P. agrimoniae*, the species studied by Ludwig and Rees, but if Plate 2, A and B, of this paper is compared with their figure 1 in Plate VIII it will be seen that the only essential difference is in the layer of somewhat shorter or more flattened subterminal cells which the author found in various stages of disorganization, indicated by the way these cells take the orange G. In their figure the subterminal cells in the four central rows are not as thick as those below them. Sections presenting such features as are shown in Plate 5, A, of this paper certainly can be interpreted to mean that the layer of cells, b, which extends across the sorus, is composed of active basal cells, since these cells take the gentian violet stain rather deeply, while the cells of the "hyphal plate" and vegetative cells below take scarcely any stain. The cells s take the orange and safranin and certainly appear to be degenerating. The cells u will develop into spores. Toward the center of this sorus space has been formed and the intercalary cell below the spore is elongating into a stock as it disorganizes. If this method of spore formation were continued, the uredospores would be borne in chains, and essentially there is very little difference between the two methods. In very compact deep-seated primordia, conditions may be such as to necessitate the formation of the first spores in this way. A greater upward thrust against the overlying tissue would result if the basal cell elongates as a whole or at its upper end in preparation for division. In Plate 5, B, are shown the first spores formed in a sorus where the pressure was soon relieved at the center by a break in the overlying tissues. Large wedge-shaped uredospores with perfectly definite stalks can be seen. Nearer the margin of this sorus there was still considerable resistance at the left and above, so that the spore initial buds developing from the basal cells, b, are pushing out to the right where the tissue was less compact. The relationship of peridial cells, p, intercalary cells, i, and basal cells, b, is very evident in sections of this sorus. Further evidence that pedicellate spores occur in more mature sori is scarcely necessary. At the right in Plate 5, C, is shown a perfectly typical pedicellate spore. At the left three adjacent basal cells are budding; nuclear division is occurring in the cell at the middle.

If the tangled mass of hyphae constituting the sorus primordium is exceptionally large the development of a clear-cut peridium is more or

less interfered with, and uredospores often appear to be formed from almost any cell of the vertically oriented hyphae. The dark area in the sorus shown in Plate 1, G, indicates where disorganization of abnormal spores or of a portion of the primordium tissue is occurring, so that space will be provided and the host tissue above ruptured. More detailed studies of the process involved in spore production in such atypical sori should be made in order to determine to what extent these apparent variations from true form are really the results of abnormal conditions.

The "hyphal plate" layer mentioned by Ludwig and Rees is commonly present along the base of the sorus in *P. americanum* and seems to be almost continuous with the peridium, as shown in Plate 1, B. The origin of this tissue is perfectly clear. The columns or chains of cells constituting the plectenchymatous primordium are the much enlarged, vertically oriented branches of the ordinary hyphae which originally formed a small tangled mass at the commencement of the uredinium. These hyphae can not be distinguished from the purely vegetative hyphae by the size, form, or staining properties of their cells. Now, the sorus increases in breadth simply by the lateral extension of branches from this undifferentiated tissue. Certain branches grow out vertically and parallel the other columns of cells and form peridial, intercalary, and basal cells in regular order, so that there are bound to be platelike layers of cells, especially along the base at the margins, which connect up with the peridium.

In order to secure further proof of the homology of intercalary cells and uredospore stalks, the author gathered and fixed material showing various stages in the development of uredinia of *P. agrimoniae* and *P. hydrangeae* on November 2 at Occoquan, Va. A study of sections of *P. agrimoniae* showed that Ludwig and Rees have given a good figure of a young sorus. There is ample evidence, on the other hand, proving that intercalary cells which degenerate are cut off below the peridium (Pl. 5, D, E) and that such cells are also formed with at least the first uredospores (Pl. 5, F). Many cases were observed where there could be no doubt that the basal cell forms one or more buds, spore initials (Pl. 5, G), each of which in turn divides to form a spore supported by a stalk. The stalk may disappear without much or any elongation. A few other stages in spore formation are figured here showing that *P. agrimoniae* does not differ materially in the organization of its uredinium from *P. americanum*.

Much of the material of *P. hydrangeae* was probably gathered too late in the season, as most of the sori sectioned had aborted or undergone degeneration after having developed the chains of cells constituting the primordium. Such stages are, in this condition (Pl. 5, J), apt to be misleading. In a few cases the uredinia appeared to be healthy and normal. Some evidence was found showing that the intercalary cells are cut off as the peridium is formed (Pl. 5, K). Certain irregularities in the structure of this tissue need further study. One could find stages where the first spores were being formed, showing that the uredospores originate as a result of the cutting off of a spore initial from the basal cell as a whole and not as a bud. In this species the cell supporting the spore must be considered the homolog of a true stalk cell or pedicel. Young spores supported by intercalary cells are shown in Plate 5, H.

Plate 3, A, B, shows more clearly that the peridium is composed of the terminal cells of the sorus primordium. The subterminals take the

orange stain more deeply than the others, therefore this layer is easily recognized in sections. Disorganization, followed by collapse, occurs, so that these interstitial cells are represented finally by more lines of degeneration products.

METHODS OF SPORE FORMATION

The formation of uredospores in Puccinia from a definite layer of basal cells which send out buds (spore initials) is well understood. Nuclear division is followed by cell division, cutting off from the spore initial the stalk cell below and the spore above. Such spores are thus not borne in chains, even though the basal cells may continue to bud and give rise to a number of spores.

Liro (*10, p. 490, 492, 493*) states that the uredospores of *Melampsorella cerastii* and *M. feurichii* are borne in caeomalike sori, that is, in chains. Magnus (*12*), while confirming Liro regarding the first species, disagrees with him as to the second, figuring stalked spores in a sorus of *M. feurichii*, and further holds that it would be impossible for a spore to be formed out of such stalk cells. He creates the new genus Milesina, especially characterized by stalked uredospores, leaving in Melampsorella *M. cerastii*, which he and Liro agree has catenulate spores.

Ludwig and Rees (*11*), who made a study of the uredinium in *P. agrimoniae*, find that the apical cells of the primordium elongate and their contents stain less deeply. The terminal cells become the first peridial cells, and the other cells of the chains are the uredospores, no intercalary cells being formed. These authors further state that the spore chains arise from a layer of basal cells just above a "hyphal plate layer," which is a tissue extending across the base of the sorus and connecting at the margins with the peridium. Stages in spore formation are not shown, although they follow Magnus in their explanation of the probable method. Since intercalary cells were not found, they suggest that the peridium is formed in a way analogous to that in the ordinary aecidium. They also suggest that the genera now included in the Pucciniastratae may be separated into two subgroups, the fern rusts having pedicellate spores in one group, and Pucciniastrum, Melampsorella, Melampsoridium, characterized by spores borne in chains with each chain maturing but one spore at a time, in the other.

The writer has not made an extensive study of the order of cell division in spore formation in *P. americanum*, but there can be no question that the uredospores are frequently borne singly on pedicels. On the other hand, if the very important fact that intercalary cells are present is disregarded, there is considerable evidence showing that the first spores, especially in deep-seated sori on petioles and canes, are borne somewhat as Magnus describes for Melampsorella. In other words, in *P. americanum* the first spore initials arise as the result of tangential divisions of basal cells and not by budding. Any claim that the upper daughter cell may sometimes become a spore at once, the sister cell remaining as a basal cell, would be difficult to disprove.

FORMATION OF THE OSTIOLE

The formation of the ostiole and the peristomal cells in *P. americanum* can be followed very readily by studying sections of sori which are not very deeply seated. About the time the first spores appear in the cavity beneath the central part of the buffer peridium, it will be seen that a few

cells at the center or apex are beginning to disorganize and collapse at their lower ends (Pl. 1, A, and 5, B). As the peridium is lifted these central cells sustain considerable pressure from the sides so that they eventually become distorted, compressed below, enlarged above, and are finally thrust somewhat out of place as they break through the epidermis. The spinelike thickenings which are being formed during the rupturing processes may in some way facilitate the final dislodgment of the peristomal cells in older sori. The cell ps in Plate 4, E, is slightly more than half the length of that of the adjacent peridial cell, p. Originally these two cells were the same length; therefore, the difference seen later is due, not to the thickening of the wall of the lower end, as thought by Farlow, but to disorganization which is not confined to the peristomal cells alone. It is interesting to see that while the lower end of such cells is becoming disorganized and distorted the cytoplasm and nuclei in the upper part are still active, holding the gentian violet stain to the last or until the spines are formed.

It is now a well-recognized fact that peridial cells of an aecium are the homologs of aeciospores, being merely the specialized terminal cells in the chain of spores. The figures in this paper suggest that these homologies can be carried over to the uredinium of Pucciniastrum, where the peridial cell and intercalary cell below are comparable to the uredospore and its stalk, which supports the theory first advanced by Sappin-Trouffy (*13, p. 86*) and further defended by Christman (*4*).

Stalked spores arising from budded basal cells were not found in the limited study of *P. hydrangeae* made by the author. Such types as are shown in Plate 5, I, suggest that in older sori the intercalary cell may elongate to take the form of a stalk and that the basal cell may bud the same as we find in the other species.

It is a certainty that spores are sometimes formed atypically in *P. americanum*, so the author has hesitated to interpret the figures in Plate 3, which show (at the right) spores without stalks or supporting intercalary cells. The author has relied on the positive evidence offered by finding intercalary cells and pedicellate spores in just such sori, rather than on such negative evidence as these figures might be interpreted to afford. In the orderly process of spore formation in uredinia there is a hymenial layer of basal cells from which spore initials regularly arise, but all sorts of abnormalities are liable to occur here as in other fungi, so that a spore might be formed from almost any cell, peridial, intercalary, or basal. Every well-nourished cell in the primordium is potentially sporogenous, but usually one of the daughter cells of the spore initial is in effect sacrificed, thus providing additional food for the one that is to become the spore; the other, although incidentally becoming a disjuncting intercalary cell or an elongated stalk, finally degenerates.[4]

Magnus' figure 7, Plate XIV (*12*), in support of his view is not convincing. He may have overlooked the stalk cells or their homologs, intercalary cells, as he did the peridial cells in Hyalopsora which Bartholomew (*3*) shows very plainly to be present in this genus. Ludwig

[4] L. Kursanov, in a recent paper which has just come to hand (Recherches morphologiques et cytologiques sur les Urédinées. Bul. Soc. Nat. Moscow, v. 31, p. 1–129, pl. 1–4, 25 fig. Oct., 1922), traces the development of terminal sterile cells in the uredo sori of *Puccinia allii*, *Triphragmium ulmariae*, *Uredo* (*Pucciniastrum*) *pirolae*, and *Hyalopsora polypodii-dryopteridis*. He figures intercalary cells directly beneath the sterile terminal cells in the last two species and states that they arise by the division of the subterminal cells. This may very well be their method of origin in the species of Pucciniastrum which the writer has under discussion, but it would not affect their homology. Instances of the cutting off of the intercalary cell from the upper part of the aecidiospore initial are well known. Kursanov has not followed fully the development of the uredo spores in *Pucciniastrum pirolae*, so that the reader is left in doubt as to whether they are provided with true stalk cells or not.

and Rees, as noted, state that the uredospores of *Pucciniastrum agrimoniae* are borne in chains and that the terminal cells of the chains elongate to become the peridial cells, the other cells developing one by one into uredospores as described by Magnus for Melampsorella. These authors did not find intercalary cells either in the spore chains or below the peridial cells. If this were true, the peridium would be formed in a manner analogous to that of the aecidium, as they pointed out.

Some of the strongest hints as to the trend in evolution are suggested by what it is thought are atypical processes; but if in addition to the method of spore formation which the author has observed in Pucciniastrum it should be rarely found that every cell below the peridium in the cell chains develops into a uredospore, as claimed by Ludwig and Rees, the doctrine of homologies would be weakened. The buffer cell in the telium of Gymnosporangium may be the homolog of the peridial cell in Puccinastrum; this depends on just how the first intercalary cell in the latter is cut off. It is not the homolog of the peridial cell of the ordinary aecidium, but rather it is comparable to the hymenial basal cell or its sister peridial initial. If the uredospores of *Melampsorella cerastii* are always borne in chains, and those of Hyalopsora are borne singly on pedicels, then the species of Pucciniastrum form a good series of connecting links, *P. hydrangeae* being more nearly like Melampsorella, especially if we should find intercalary cells in the latter.

The complete life history of *P. americanum* is unknown. Three other species of the genus have their aecial stage on Tsuga and two on Abies. The occurrence of our rust on canes of the current season suggests that the fungus may live through the winter, thus obviating the necessity for the alternate aecial stage in certain localities. No explanation has been offered to account for the presence of the deep-seated, inverted sori on canes, which are very common. It is possible that the inversion may facilitate spore discharge the following spring as the cortical parenchyma peels off, exposing the cork tissue below. Such inverted sori were not found on leaves or petioles.

It has been shown that the form and size of sori vary greatly, depending upon what tissue they are found, indicating that *P. arcticum* and *P. americanum* are not distinct species. In the event that it can be shown that *Rubus triflorus* and *R. arcticus* can not be infected with spores from *R. strigosus* and related forms, distinct names for the strains or biologic forms might still be desirable.

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PLATE 1[a]

Pucciniastrum americanum (Farl.) Arth. on June × Cuthbert Red Raspberry

A.—Section through the center of a young uredinium on leaf stalk. Four layers of host cells lie above the sorus. Cells next to the sorus have been crushed by the expansion of the buffer tissue. Disorganization of cells at the center. Uredospores formed irregularly, intercalary cell replaces stalk.

B.—Vertical section through a mature sorus on a leaf stalk. Only two layers of host cells above. The buffer tissue has been flattened by the pressure from within and will persist more or less as a peridium, although the cells at the center are fully collapsed and will soon disappear. No corona would have been formed. Uredospores stalked.

C.—Vertical section of sorus on lower side of leaf. One cell of the corona showing.

D.—Inverted broadly elliptical sorus on young cane. "Peridium" or buffer tissue facing the cork cambium, which is deep-seated; e, epidermis; ck, cork layers.

E.—Inverted sorus still more deeply seated. Buffer tissue directly against the cork.

F.—Two lenticular sori on a cane. The upper one lies just beneath the epidermis and is erect; the lower is inverted.

G.—Erect double sorus on large cane. Peridium of the part at the left has entirely disappeared, cavity filled with spores. At the right peridium still evident although disorganizing. Degeneration of tissue at the center of the sorus (dark area), normal spore production below. Note the position of the epidermis above the sorus and of the cork cambium below it; e, epidermis, cp, cortical parenchyma, ck, cork.

B to F, photographed with Leitz 8 mm. lens and No. 10 oc.; A, 4 mm., 6 oc.; G, 16 mm., 10 oc.

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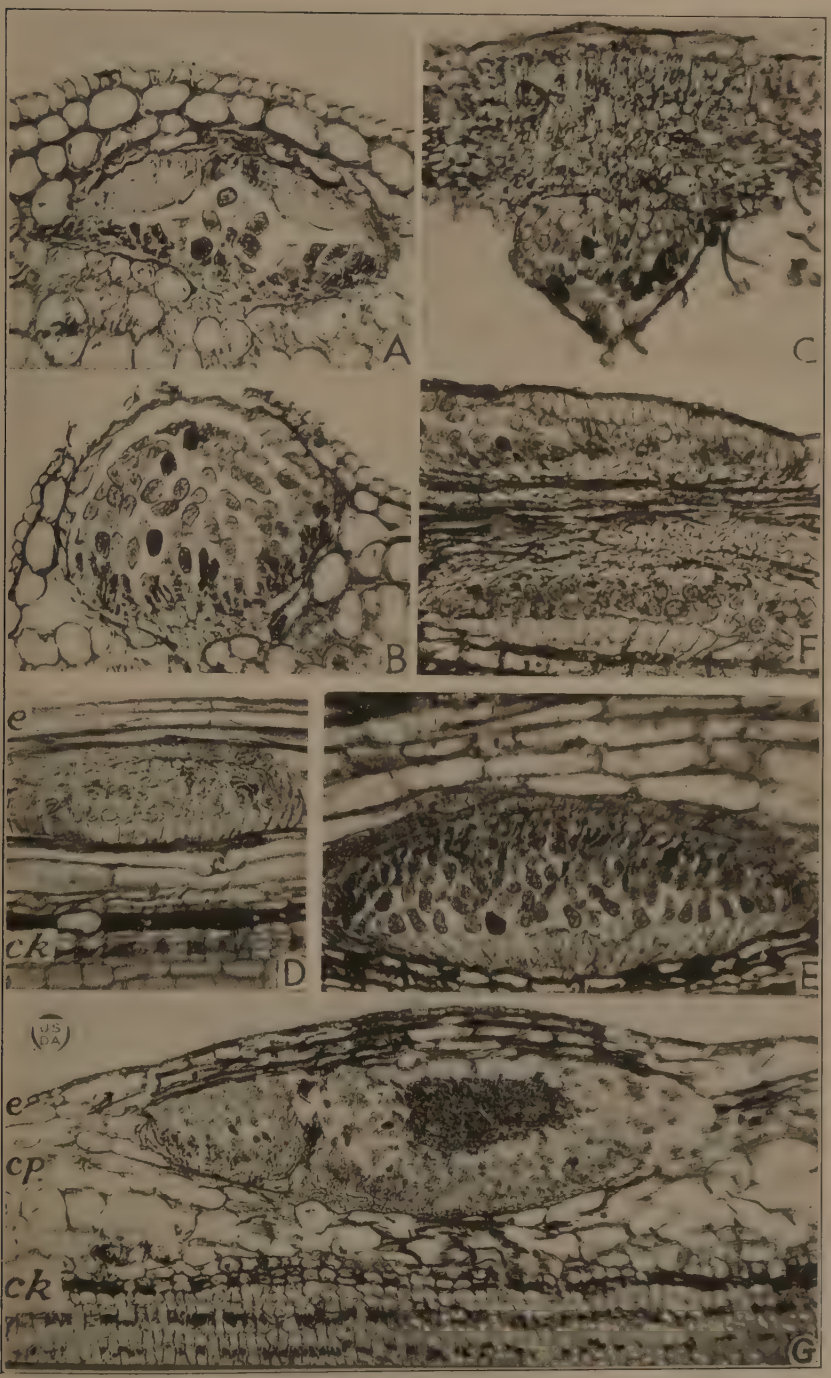
[a] The photographs shown in Pl. 1, and all the sections which were studied in the preparation of this paper were made by Miss Ruth Colvin.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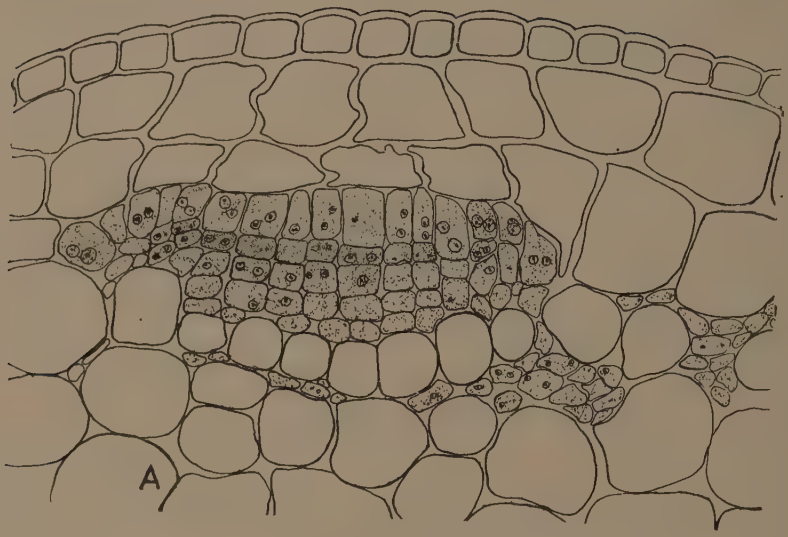

A

B

PLATE 2

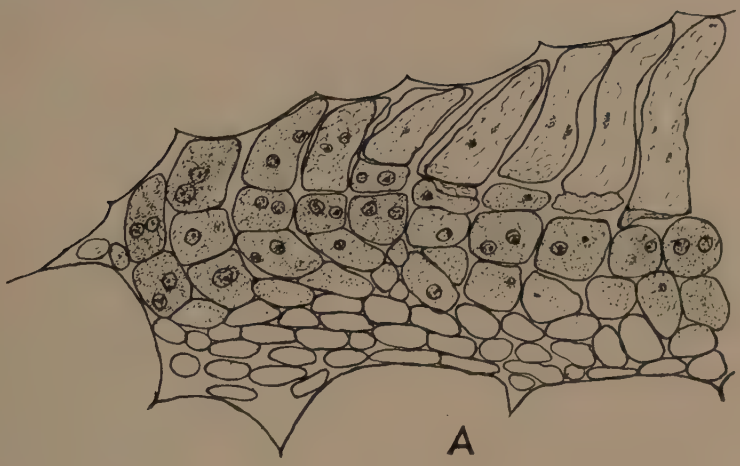
A.—Primordium of sorus on leaf stalk of raspberry, showing its position in the host tissues. Peridial or buffer cells, each accompanied by a disorganizing intercalary cell, at the center of the sorus. Cell division by which intercalary cells are formed has not occurred at the margins.

B.—Primordium of sorus on petiole of raspberry. Terminal cells elongating, intercalary cells disorganizing. Cells at the margin just before division.

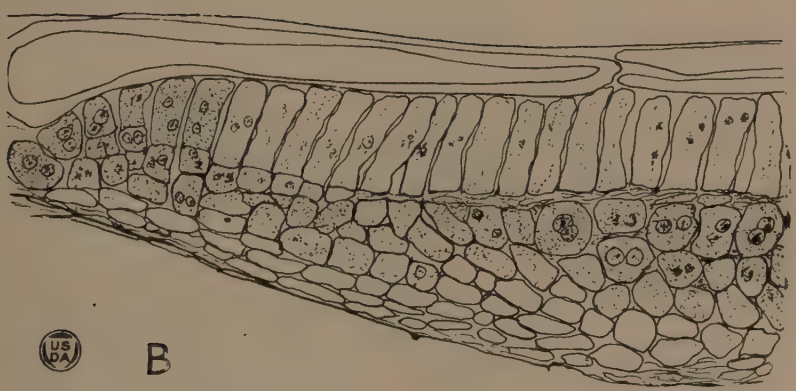
PLATE 3

A.—Part of section of a young sorus on leaf stalk. Peridial cells fully elongated at the right, contents disappearing, intercalary cells collapsing.

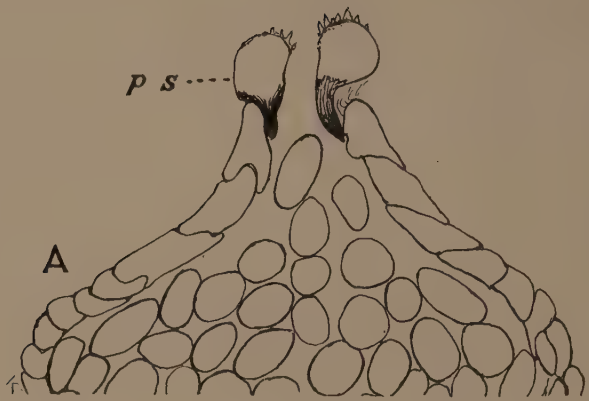
B.—Part of section of a small and rather flat sorus on a cane. Buffer tissue of erect cells; intercalary cells in all stages of disorganization. Five uredospores at right center.



A



B


P S
A

B

C

D

P S
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E

PLATE 4

The origin of peristomal cells in *P. americanum*. Deep shading of the peristomal cells, PS, indicates disorganization; P, peridial cell. (See text for further explanation.)

PLATE 5

P. americanum

A.—Columns of cells in a young, compact sorus. Uredospores arise by division of spore initial cells: p, peridial cell; i, intercalary cell; u, uredospore; s, stalk; b, basal cell.

B.—Formation of stalked spores in a sorus in which space was provided by the early rupture of overlying tissues. Spore initial buds are arising from basal cells (at the left) so that the first spores will be borne on stalks.

C.—Uredospores formed from budding basal cells. Nuclear division occurring in the bud from the second basal cell.

P. agrimoniae

D.—Row of cells at margin of sorus, wedge-shaped intercalary cell below the peridial cell p.

E.—Fully elongated peridial cells supported by intercalary cells beneath which are normal basal cells, not spores.

F.—Typical spore initial bud si, from basal cell (right); cell chain consisting of young uredospore, intercalary cell, basal cell, and "hyphal plate" cell; stalked spores.

G.—Short stalk cells. Whether we find two spores or only one connected with the basal cell may depend on the way the cell is sectioned.

P. hydrangeae

H.—Four young uredospores, u, each supported by an intercalary cell.

I.—Intercalary cell elongating somewhat.

J.—Chains of cells in an aborted sorus. Intercalary cells beneath the peridium.

K.—Cell chains at the margin of a normal young sorus; wedge-shaped intercalary cells degenerating.

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